

## Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake nutrient manipulations

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**Abstract.** Substratum heterogeneity is a large source of variability in periphyton production, but the influence of substratum on periphyton response to experimental manipulations is rarely measured. Using laboratory and whole-lake experiments, we compared area-specific primary production of periphyton on wood (epixylon) and sediment (epipelon), and tested whether periphyton on the 2 substrata responded differently to water-column fertilization. In the laboratory, natural periphyton assemblages on wood or sediment were exposed to 1 of 6 treatments in a fully factorial (light [250, 70, or 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ]  $\times$  nutrient [control or + N and P]) experiment. We measured  $^{14}\text{C}$  primary production on both substrata after 25 to 30 d. We also measured epipellic and epixylic production in a reference and an experimentally fertilized lake. We constructed photosynthesis-irradiance curves for epipelon from 3 depths in each lake, and used the curves to predict primary production at average in situ light intensities for each lake and depth.

Production response to fertilization was substratum-specific, and area-specific epipellic production was 10 $\times$  that of epixylon at both experimental scales. Both epixylon (ANOVA,  $p < 0.0001$ ) and epipelon (ANOVA,  $p < 0.0001$ ) production increased significantly with increasing light. Epixylon production was significantly higher in fertilized treatments than in controls (ANOVA,  $p < 0.01$ ), but epipelon did not respond to fertilization (ANOVA,  $p = 0.69$ ). Epixylon production was also significantly higher in the fertilized lake than in the reference lake (ANOVA,  $p < 0.05$ ). Maximum epipellic production rates decreased with water depth in both lakes, and average epipellic production from both lakes was positively and similarly related to average in situ light intensities (linear regression,  $R^2 = 0.94$ ,  $p = 0.001$ ). Both substratum-specific response to fertilization and substratum-specific periphyton production may be critical in determining fertilization-induced changes in periphyton production in lakes.

**Key words:** periphyton, substratum, primary production, epipelon, epixylon, nutrients, light, lakes.